

# Effects of Javan Rusa Deer (*Cervus timorensis*) on Native Plant Species in the Jibbon-Bundeena Area, Royal National Park, New South Wales

DAVID KEITH<sup>1</sup> AND BELINDA PELLOW<sup>2</sup>

<sup>1</sup>NSW Department of Environment and Conservation, PO Box 1967, Hurstville 2220 NSW.

<sup>2</sup>Janet Cosh Herbarium, University of Wollongong, Wollongong 2522 NSW.

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A reconnaissance survey and enclosure experiment were carried out to examine the effects of Javan rusa deer on native flora and vegetation in Royal National Park on the southern outskirts of Sydney, Australia. Of 78 native plant species examined during the survey, only nine showed no evidence of vertebrate herbivory or physical damage and the majority of these plants were ferns and sedges. The other 69 species showed effects that included defoliation (young and/or old leaves), removal of shoots, bark-stripping, stem breakages and destruction or consumption of reproductive material. These effects varied in severity between species and from place to place, and were inferred to have been caused by deer based on the local abundance of deer droppings, footprints and the scarcity of other vertebrate herbivores in the area. The survey also revealed localised soil erosion associated with high densities of deer footprints and droppings. An unreplicated enclosure experiment showed that planted saplings of *Syzygium paniculatum*, a threatened rainforest tree, suffered major defoliation, bark stripping, stem breakages and some mortality when exposed to deer for several months. Many of the surviving plants showed signs of recovery when deer were subsequently excluded, although full recovery of their leaf canopies could take several seasons. The observed effects on vegetation and individual plant species are consistent with studies on several other deer species in a range of ecosystems overseas. A model of the effects of deer herbivory based on plant life-history suggests that curtailment of seed production and seedling recruitment are likely to be the major impacts of deer on plant population viability. Reductions in net growth and survival of established plants and possibly post-dispersal predation of seeds are less likely to be significant influences.

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## INTRODUCTION

Javan rusa deer (*Cervus timorensis*) is one of six deer species that have established wild populations in Australia (Moriarty 2004a). Rusa deer were introduced into Royal National Park in 1906 by the Park Trust for exhibition purposes (NSW National Parks and Wildlife Service 2002). The seven introduced animals were initially kept within a fenced enclosure at 'Deer Park' on the Hacking River near Warumbul. The deer soon escaped and established a wild population that has persisted in the Park and adjacent areas to the present day. Hamilton (1981) suggested that rusa deer essentially replaced fallow

deer (*Dama dama*), which were introduced some 20 years earlier and likely to be the species reported as widespread in the Park in 1914 (Anon. 1914). High densities of Rusa deer are now regularly observed in the vicinity of Bundeena, Grays Point, Garie-Era and various sites along the Hacking River valley. The deer population is likely to have fluctuated since its introduction, although densities appear to have increased markedly since bushfires in January 1994, which burnt more than 90% of the Royal National Park (pers. obs.). After the fires, the population within Royal National Park was estimated to include less than 500 individuals. Quantitative surveys carried out between 1999 and 2001 indicate that the population

## METHODS

increased from 2500 to 2900 individuals during that time (Moriarty unpubl. data, NSW National Parks and Wildlife Service 2002).

Rusa deer grow to 1 m tall at the shoulder and weigh 100-160 kg. Males develop large antlers but females do not. The deer are active nocturnally, resting in dense native vegetation by day. They are dietary opportunists, apparently preferring grass but browsing opportunistically on the buds, shoots and leaves of woody plants and herbs (Bentley 1979). Recent dietary data from Royal National Park indicate that food sources vary with season and location. In native vegetation remote from settled areas, 80% of their average summer diet consists of native browse, with grasses making up the remaining 20% (Moriarty 2004b). In other seasons, the grass component becomes negligible in these areas. However, the grass component varies seasonally from 40% to 70% in animals living close to cleared grassy areas (Moriarty 2004b).

Concerns about impacts on native vegetation have resulted in a recent preliminary determination of feral deer as a Key Threatening Process under the *NSW Threatened Species Conservation Act 1995*. A recent survey of rangers employed by Rural Lands Protection Boards in NSW identified deer as the most important emerging pest animal threat (West and Saunders 2003). More than 40% of respondents indicated that there had been a moderate to high increase in the distribution and abundance of wild deer in their area. In another recent survey more than 80% of land managers reported browsing of native plants and agricultural crops as an impact of feral deer (Moriarty 2004a). Despite numerous detailed studies on the impacts of deer on native vegetation in other countries (e.g. Okuda and Nakane 1990, Veblen et al. 1992, Kay 1993, Jane 1994, Anderson and Katz 1993, Mladenoff and Stearns 1993, Khan et al. 1994, Augustine and Frelich 1998, Akasi and Nakashisuka 1999, McShea and Rappole 2000, Fuller and Gill 2001, Coomes et al. 2003, Rooney et al. 2004), there are relatively few published data from Australia on this subject. In Royal National Park and adjacent urban areas, the high densities of deer, their free movement in open areas and their exclusion from some properties provide opportunities to examine the effects of deer on native vegetation. The aims of this study were to document the various impacts of deer on native vegetation, compile a list of native plant species affected by deer and to quantify the effects of deer on a threatened plant species, *Syzygium paniculatum*.

### Study area

Jibbon-Bundeena is a 300 ha area located in the far north-east corner of Royal National Park on the shores of Port Hacking on the southern outskirts of Sydney (lat. 34° 06'S, long. 151° 09'E). The bedrock of Hawkesbury sandstone is overlain in some parts by podsolised marine and aeolian sand dunes that may exceed 10 m in depth. The dune crests and slopes are freely drained, although the swales and flats may be periodically waterlogged. The exposed sandstones carry shallow to skeletal yellow earths with variable drainage characteristics.

The area includes a mosaic of rainforests, eucalypt forests, heathlands and wetlands. Littoral rainforest on the hind dunes of Jibbon and Bonnie Vale beaches is dominated by *Cupaniosis anacardioides* with *Acmena smithii*, *Glochidion ferdinandi* subsp. *ferdinandi* and *Banksia integrifolia* subsp. *integrifolia*. It forms part of an Endangered Ecological Community (Littoral Rainforest in NSW) under the *NSW Threatened Species Conservation Act 1995* and includes *Syzygium paniculatum*, which is currently listed as a Vulnerable species. The eucalypt forests are found principally on deep sands. On dune slopes they are dominated by *Corymbia gummifera* and *Angophora costata* with an understorey of sclerophyllous shrubs and bracken. On sandy flats, *Eucalyptus botryoides* and *A. costata* form a taller forest with an understorey that includes a mixture of mesophyllous and sclerophyllous shrubs and herbaceous plants. Heathlands occur on deep sands and on the exposed sandstone plateau. Floristic composition varies between these substrates, although both communities comprise a dense to open cover of sclerophyll shrubs interspersed with sclerophyll sedges. Wetlands are restricted to lagoons in dune swales and swampy sand flats. They are mainly herbaceous communities dominated by *Baumea juncea* with *B. articulata*, *Leptocarpus tenax* and other sedges. They are currently listed as an Endangered Ecological Community (Sydney Freshwater Wetlands) under the *NSW Threatened Species Conservation Act 1995*.

The township of Bundeena occupies about 100 ha within the study area, covering sand dunes, sand flats and sandstone ridges. The majority of the town precinct comprises suburban dwellings on blocks <0.1 ha, some of which are fenced to exclude deer from gardens. There are substantial areas planted with exotic grass on road verges and in parks and yards. Native plants, relics of the original vegetation, persist as solitary individuals or in clumps throughout the town. At least some of the deer in the area spend

some of their nocturnal foraging time within the suburban limits of Bundeena. They graze on grassy areas and are fed vegetable matter by a few local residents. They also browse on a variety of forbs and woody plants, including various vegetables, exotic ornamental plants and local native plants.

### Survey

Extensive reconnaissance was undertaken throughout the native vegetation and the suburban area to observe deer behaviour and movement, record plant species consumed or damaged by deer and effects of deer on the structure of vegetation and soils. Observations were made opportunistically between 1999 and 2003. Observations on native plants were confined to bushland areas within 1 km of Bundeena township, but at least 20 m beyond the suburban/bushland boundary. The effects were classified into the following categories: young foliage and shoots consumed; young and old foliage and shoots consumed; bark stripped; woody stems broken; seedlings uprooted; inflorescences damaged or consumed; and unaffected. Qualitative observations on damage to vegetation structure and soils were also recorded during the reconnaissance of bushland.

To examine the effects on soils where deer activity was concentrated, three sites were identified where deer were fed by local residents. All three sites were on deep, unconsolidated sand dune soils on the interface between eucalypt woodland and the eastern edge of the suburban area. They were separated from one another by distances of 200 metres, and not included in the reconnaissance survey, which sampled bushland away from the suburban interface. Soils and vegetation at these sites were observed between 1999 and 2003, and qualitative descriptions of vegetation cover and soil level were compared to those of equivalent sites on the bushland/suburban interface approximately 50 m distant from each feeding site. The equivalent sites were also on sand and had similar vegetation (disturbed heathy woodland) and a similar management history to the feeding sites.

### Exclosure experiment

Ninety-three individuals of *Syzygium paniculatum* were planted in a 0.1 ha yard, grassed with *Pennisetum clandestinum* and enclosed within 1 m high wire fencing. The plants were 1.0 – 1.4 m tall and were watered for three months after planting. After one month, all plants were in a healthy condition and growing new shoots when the yard was opened, allowing deer access. Initially relatively few deer entered the yard, but after several weeks, several animals gained regular access during nights. After three

months, the gate was closed. Deer gained intermittent access to the yard after that time until the perimeter fence was raised to a height of 1.5 m. As a qualitative control treatment, five plants were observed in an adjacent yard that was maintained to exclude deer throughout the duration of the experiment. Brush-tailed possums, the only other vertebrate herbivore on the site, were observed in both the treatment and control yards. Effects on *Syzygium paniculatum* were recorded six months after deer initially gained access as follows: >75% foliage and branchlets consumed; ≤75% foliage and branchlets consumed; main stem broken within 30 cm of base; bark removed; or foliage and branches unaffected. One year after deer had been excluded, plants were recorded as either dead, alive and growing new shoots or alive and not growing new shoots.

## RESULTS

### Vegetation structure and soils

Reconnaissance of bushland suggested that structural irregularities in the vegetation, including tracks and open areas with low densities of woody plants, were associated with deer access and activity. Footprints indicated that a number of tracks in the area were used by both humans and deer. However, numerous tracks in the area showed no evidence of regular human usage and generally dissipated after some distance or terminated in open areas in the forest understorey or heathland. These open areas varied from 2 – 50 m<sup>2</sup> and had conspicuously lower densities of shrubs and groundcover than the surrounding vegetation (Fig. 1a). Resting deer were disturbed from some of these sites during reconnaissance and the presence of droppings, footprints and/or dead remains of deer at most sites suggested that they function as deer encampments. There was little evidence of significant surface erosion on the sand dunes within heathlands or woodlands, except along the tracks (Fig. 1b), which were depressed below the general soil surface. However, the wetland soils were exposed, compacted and deformed on the surface by deer footprints. These areas of bare compacted soil were most commonly encountered around the margins of wetlands.

The three sites where deer were fed by local residents on the bushland/suburban interface had a low open cover of grasses, herbs and shrubs when observations began in 1999. By 2003, all three sites were denuded of vegetation cover and had lost up to 0.6 m of topsoil (Fig. 2). At two of the sites, retaining walls supporting built-up residential yards had been



**Figure 1. Changes in the structure of vegetation and soils related to deer activity: a (top) clearing approximately 220 m east of Bundeena within a dry sclerophyll forest from which all woody understorey plants have been eliminated and groundcover plants have been thinned exposing bare soil; b (bottom) an area near the beginning of the coast walk opened up by deer activity approximately 6 months prior to photograph, showing deer footprints on bared soil surface and lignotubers of *Lambertia formosa* exposed by significant soil erosion.**



**Figure 2.** Site on the bushland/suburban interface at the end of Scarborough Street, Bundeena, where concentrated deer activity resulted in substantial loss of soil. The relic shrub with exposed root burl is *Leucopogon ericoides*. Feeding of deer ceased at this site approximately two years prior to photograph, though the animals continue to pass through the area and maintain an exposed soil surface.

substantially undermined by erosion of the dune. The denuded areas had high densities of deer droppings and footprints, and varied in area from 400 to 1075 m<sup>2</sup>. The roots of trees and large shrubs (*Corymbia gummifera*, *Banksia integrifolia* subsp. *integrifolia*) had been exposed and broken in the eroded sites. Substantial volumes of sand had been transported downslope and deposited within the adjacent area of native vegetation. The equivalent sites on the bushland/suburban interface, approximately 50 m from each of the feeding sites, showed lower densities of deer prints and dung, comparatively little evidence of erosion and sedimentation, and retained an open continuous cover of grasses, herbs and scattered shrubs.

#### Plant survey

Seventy native plant species from 29 families and two introduced species showed evidence of damage by deer (Table 1). Young foliage and shoots were preferentially browsed on most of the plant species recorded. Older and tougher leaves were less affected, although in many species there appeared to be little distinction between consumption of young and old leaves (Fig.3). The effects of browsing were spatially variable because some species that

were heavily browsed in some areas appeared to be relatively unaffected in others. The removal of shoots was particularly frequent and conspicuous in many leguminous species (family Fabaceae), with some individuals being completely defoliated. Rainforest species, notably *Acmena smithii*, *Cissus antarctica*, *Clerodendrum tomentosum*, *Rapanea howitteana* and *Syzygium paniculatum*, also suffered high levels of defoliation. The plant families Epacridaceae and Proteaceae also had large numbers of affected species.

Bark was removed or damaged on large woody stems of six species (Table 1). In some cases, scattered remains of bark and the abraded appearance of the stem from which bark was removed suggested that damage was probably caused by antler rutting. In other cases, particularly the rainforest species, bark had been torn off in strips and may have been consumed as food. In several monocotyledonous species, including orchids, *Doryanthes* and *Xanthorrhoea*, inflorescences had been consumed or destroyed. Remains of destroyed *Xanthorrhoea* inflorescences indicated that this occurred during the bud stage. Only nine species of plant consistently showed no evidence of damage by deer. Three of these were ferns and three were sclerophyllous sedges.

Family	Species	Young foliage and shoots consumed	young and old foliage and shoots consumed	Bark stripped	Woody stems broken	Seedlings uprooted	Inflorescences damaged or consumed	Not affected
Agavaceae	<i>Doryanthes excelsa</i>	X					X	
Anacardiaceae	<i>Euroschinus falcata</i>	X						
Anthericaceae	<i>Thysanotus virgatus</i>		X				X	
Apiaceae	<i>Platysace linearifolia</i>		X					
Arceaceae	<i>Livistona australis</i>	X				X		
Asparagaceae	* <i>Asparagus densiflorus</i>		X					
Casuarinaceae	<i>Allocasuarina distyla</i>	X						
Casuarinaceae	<i>Casuarina glauca</i>	X			X			
Cyperaceae	<i>Caustis pentandra</i>	X						
Cyperaceae	<i>Lepidosperma concava</i>	X						
Cyperaceae	<i>Schoenus brevifolius</i>							X
Dennstadiaceae	<i>Pteridium esculentum</i>							X
Dennstadiaceae	<i>Hypolepis muelleri</i>							X
Dilleniaceae	<i>Hibbertia scandens</i>		X					
Elacocarpaceae	<i>Elaeocarpus reticulatus</i>	X						
Epacridaceae	<i>Astroloma pinifolia</i>	X?						
Epacridaceae	<i>Brachyloma daphnoides</i>		X					
Epacridaceae	<i>Epacris longiflora</i>	X						
Epacridaceae	<i>Leucopogon ericoides</i>	X						
Epacridaceae	<i>Leucopogon parviflorus</i>	X						
Epacridaceae	<i>Monotoca elliptica</i>	X?						
Epacridaceae	<i>Monotoca scoparia</i>	X						
Epacridaceae	<i>Styphelia viridis</i>		X					
Euphorbiaceae	<i>Phyllanthus gunnii</i>	X?		X				
Euphorbiaceae	<i>Ricinocarpus pinifolius</i>		X					
Fabaceae	<i>Acacia implexa</i>	X						
Fabaceae	<i>Acacia longifolia</i>		X					
Fabaceae	<i>Acacia suaveolens</i>		X					
Fabaceae	<i>Aotus ericoides</i>		X					
Fabaceae	<i>Bossiaea ensata</i>	X						
Fabaceae	<i>Bossiaea heterophylla</i>		X					
Fabaceae	<i>Dillwynia floribunda</i>	X						
Fabaceae	<i>Kennedia rubicunda</i>		X					
Fabaceae	<i>Phyllota phyllicoides</i>		X					
Fabaceae	* <i>Senna pendula</i> var. <i>glabrata</i>		X					
Fabaceae	<i>Viminaria juncea</i>		X?					
Iridaceae	<i>Patersonia glabrata</i>	X						
Lomandraceae	<i>Lomandra longifolia</i>	X						
Luzuriagaceae	<i>Geitonoplesium cymosum</i>		X					
Moraceae	<i>Ficus rubiginosa</i>		X					
Myrsinaceae	<i>Rapanea howitteana</i>		X					
Myrtaceae	<i>Acmena smithii</i>		X					
Myrtaceae	<i>Angophora costata</i>	X				X		
Myrtaceae	<i>Corymbia gummifera</i>	X?		X	X		X	
Myrtaceae	<i>Leptospermum laevigatum</i>		X					
Myrtaceae	<i>Leptospermum polygalifolium</i>	X						
Myrtaceae	<i>Leptospermum squarrosium</i>		X					
Myrtaceae	<i>Leptospermum trinervium</i>		X					
Myrtaceae	<i>Melaleuca nodosa</i>							X
Myrtaceae	<i>Syzygium paniculatum</i>		X	X				

Family	Species	Young foliage and shoots consumed	young and old foliage and shoots consumed	Bark stripped	Woody stems broken	Seedlings uprooted	Inflorescences damaged or consumed	Not affected
Oleaceae	<i>Notelea longifolia</i>	X						
Orchidaceae	<i>Caladenia caerulea</i> <sup>+</sup>						X	
Orchidaceae	<i>Cyrtostylis reniformis</i> <sup>+</sup>						X	
Orchidaceae	<i>Glossodia minor</i> X						X	
Orchidaceae	<i>Caladenia caerulea</i> hybrids <sup>+</sup>							
Orchidaceae	<i>Pterostylis</i> sp. <sup>+</sup>						X	
Phormiaceae	<i>Dianella caerulea</i>	X						
Poaceae	<i>Auustrospica pubescens</i>		X					
Proteaceae	<i>Banksia ericifolia</i>							X
Proteaceae	<i>Banksia integrifolia</i> subsp. <i>integrifolia</i>	X	X					
Proteaceae	<i>Banksia marginata</i>		X					
Proteaceae	<i>Banksia oblongifolia</i>		X					
Proteaceae	<i>Banksia serrata</i>	X		X				
Proteaceae	<i>Conospermum taxifolium</i>		X					
Proteaceae	<i>Hakea laevipes</i> subsp. <i>laevipes</i>		X					
Proteaceae	<i>Hakea propinqua</i>				X			
Proteaceae	<i>Isopogon anemonifolius</i>	X						
Proteaceae	<i>Lambertia formosa</i>							X
Proteaceae	<i>Persoonia levis</i>		X					
Proteaceae	<i>Petrophile pulchella</i>		X					
Proteaceae	<i>Telopea speciosissima</i>	X					X	
Proteaceae	<i>Xylomelum pyriforme</i>		X					
Restionaceae	<i>Hypolaena fastigata</i>							X
Restionaceae	<i>Leptocarpus tenax</i>							X
Rutaceae	<i>Acronychia oblongifolia</i>	X		X				
Sapindaceae	<i>Cupaniopsis anacardioides</i>	X						
Sinopteridaceae	<i>Pellaea falcata</i> var. <i>falcata</i>							X
Solanaceae	<i>Solanum stelligerum</i>	X?						
Ulmaceae	<i>Celtis paniculata</i>			X	X			
Verbenaceae	<i>Clerodendrum tomentosum</i>		X					
Vitaceae	<i>Cissus antarctica</i>	X						
Vitaceae	<i>Cissus hypoglauca</i>	X						
Xanthorrhoeaceae	<i>Xanthorrhoea resinifera</i>						X	

\* Introduced species

<sup>+</sup> Margaret Bradhurst, unpubl. data.

Table 1. (opposite page and above) List of plant species affected by deer. Nomenclature follows Harden (1990-2002) and recent updates ([www.plantnet.rbgsyd.gov.au](http://www.plantnet.rbgsyd.gov.au)).

### Effects on *Syzygium paniculatum*

All 93 individuals of *Syzygium paniculatum* suffered some loss of foliage when deer gained access to the yard (Table 2). For a large majority of individuals, the level of defoliation was severe, with less than 25% of foliage remaining on the plant. About 15% of plants were severely damaged, having their bark stripped off or their main stem broken near ground level. However, about 90% of plants began

to recover when deer were excluded, shooting new foliage in the next growing season. The five plants in the adjacent yard, where deer remained excluded, did not suffer any appreciable loss of foliage. Scats and nocturnal observations indicated that deer regularly gained access to the open yard, but not to the closed control, while common brush-tailed possums gained access to both yards and were the only other vertebrate herbivore observed at the site.



**Figure 3.** Defoliation caused by deer herbivory on shrubs of (a - upper left) *Styphelia viridis* subsp. *viridis*; (b - upper right) *Leptospermum squarrosum*; (c - lower left) *Banksia marginata*; (d - lower right) *Persoonia levis*. Various heathland sites on sand ca. 400-500 metres from the eastern fringe of Bundeena.



Effect class	Control	Treatment 6 months after deer gained access	Treatment one year after deer gained access and were subsequently excluded		
	Number (%) of plants (N=5)	Number (%) of plants (N=93)	Alive & sprouting new foliage	Alive but with no new foliage	Dead
>75% foliage and branchlets consumed	0	78 (84)	72	5	1
≤75% foliage and branchlets consumed	0	3 (3)	3	0	0
main stem broken within 30 cm of base	0	9 (10)	7	1	1
bark removed	0	3 (3)	2	0	1
foliage and branches unaffected	5 (100)	0 (0)	-	-	-

**Table 2. Effects of deer on planted *Syzygium paniculatum* in the enclosure experiment.**

## DISCUSSION

Deer consumed a wide variety of plant material including young and old foliage, branchlets, bark and reproductive material of a large number of plant species from a broad taxonomic spectrum. The generalisation that deer limit regeneration and reproduction in a wide variety of plant species appears to hold for different species of deer studied across a broad range of ecosystems all over the world, including North America (McShea and Rappole 1999, Opperman and Merenlender 2000, Rooney 2001, Rooney et al. 2004), Europe (Kay 1993, Fuller and Gill 2001, Rackham 2003) and Asia (Okuda and Nakane 1990, Kahn et al. 1994, Akasi and Nakashisuka 1999), where deer are native, and Australia (Moriarty 2004a), New Zealand (Jane 1994, Coomes et al. 2003) and South America (Veblen et al. 1992), where they have been introduced. In both cases, deer populations seem to have increased recently, either as a result of expansion into new habitats at previously uninhabited locations (Forsyth et al. 2004) or as a result of landscape changes within their natural range (Mladenoff and Stearns 1993, Fuller and Gill 2001). The large number and diversity of native plant species affected by deer in the Bundeena-Jibbon area were also consistent with previous studies in Royal National Park that have shown deer to be adaptable dietary generalists. Hamilton (1981), for example, showed that the proportion of food types consumed by deer varied with season and habitat. Deer faeces generally contained higher proportions of shrub and herb fragments in winter and/or spring, and higher proportions of grass fragments in other seasons. Faeces recovered from rainforest had the highest content of shrub and herb material (ca. 80%), while faeces from grassland/wet sclerophyll habitats had

the highest content of grasses (70-90%) and faeces from dry sclerophyll forest and heathland had roughly equal proportions of broad-leaf and grass material. Moriarty (2004b) recorded similar dietary variation from rumen analyses, with grasses comprising the majority of food in the vicinity of cleared areas, while native plants other than grasses were the major food source in other areas.

Our list of plant species affected by deer is substantially larger than previously reported lists (Hamilton 1981), but most unlikely to be exhaustive. Uncommon species and herbaceous species, which may be consumed in their entirety, are likely to be under-recorded in reconnaissance surveys such as ours. There is also a risk that signs of browsing could have been overlooked on some plants or that evidence of browsing was erroneously attributed to deer. The latter source of errors is unlikely to be significant because wallaby and possum scats were rarely seen within the study area, whereas deer scats were very common. Alternative techniques entail different sampling errors. Analyses of faeces and rumen samples, for example, face difficulties of identifying plant fragments, high variability between samples and limitations that labour-intensive laboratory analysis impose on sample size. Nevertheless, it would be possible to compile a more comprehensive list of plants consumed by deer with increased sampling effort and a combined sampling approach including enclosure experiments and analyses of faeces and rumen.

In addition to the direct effects of herbivory, deer had substantial, though localised, impacts on soils and vegetation structure. Dune soils were severely eroded at parts of the urban interface where feeding by humans lead to intensive deer activity. The comparison with equivalent sites nearby indicated that the severe impacts diminish rapidly with distance from feeding sites. However, destabilisation of the dune may result

in the longer term if the denuded sites become the catalyst for more widespread mobilisation of sand. Within native vegetation, shrub cover was locally reduced along deer tracks and in encampment areas but erosion of sand was generally minimal. Impacts on wetland soils were more marked, with increased exposure, compaction and surface deformation evident in all three wetlands inspected.

The enclosure experiment showed that deer may have very substantial impacts on the populations of at least some plant species over a relatively short time frame. The extent of foliage and shoot removal precluded any chance of reproduction in the plants exposed to browsing by deer. The level of mortality caused by bark stripping and stem breakages, while comparatively small over the duration of the experiment, would account for an appreciable reduction in a cohort of saplings over several years. The combined effects of foliage and shoot removal and cumulative mortality are likely to delay or prevent the growth of individual plant canopies above the browse height. *Syzygium paniculatum* appears to be one of the more palatable native plants in the study area, despite the essential oils in its foliage and the availability of copious grass in the vicinity. The observed effects on *S. paniculatum* probably represent the more severe of those to be observed among wild plant populations although, in bushland, severe defoliation was observed in species from a wide range of plant families including Fabaceae and Epacridaceae (Fig. 2). Effects are likely to be particularly severe in rainforest communities, such as the Littoral Rainforest Endangered Ecological Community. They also have major implications for revegetation projects, which may be prone to major losses if deer gain access to the plantings before they grow beyond browse height (e.g. Opperman and Merenlender 2000).

A number of limitations in the design of the enclosure experiment impose constraints on interpretation of the results. The comparison was based on unreplicated treatments with unbalanced sample sizes. In the field, plants would be exposed to deer browsing at a much younger stage and would not be surrounded by grassy areas as they were in our experiment. Despite these differences between the experimental conditions and those in the field, the symptoms of deer browsing observed in the experimental population were substantial (relative to the control plants) and similar to those observed in other rainforest and sclerophyll forest plant species during reconnaissance of native vegetation. Data from replicated enclosures, which have recently been established in native vegetation (Moriarty 2004b),

will help to resolve uncertainties that arise when interpreting our experimental results in the context of wild plant populations.

In Fig. 4, we propose a model of impacts based on plant life histories as a means of structuring future experimental investigations on the medium- to long-term impacts of deer herbivory on native vegetation. The model proposes that deer herbivory has its largest impact on population viability by interrupting two major plant life-cycle processes: seedling establishment and seed production. Compared with established plants, seedlings have less capacity to recover after defoliation and could be more palatable due to the lower content of fibre, tannins and phenolic compounds in their leaves. Bushfires expose more seedlings to browsing by deer because they release seeds of many species from dormancy or canopy storages (Keith 1996). Populations of plant species that only regenerate from seed are exposed to greater risks of decline than those in which a proportion of pre-fire established plants survive. Factors that influence the density of post-fire deer populations, such as fire size and patchiness and deer dispersal patterns, are potentially important in mediating the impact of deer on seedling recruitment.

A second mechanism of deer impact on the viability of plant populations is through the reduction of fruit production (Fig. 4), as the resulting decline in seed banks reduces the capacity for seedling recruitment. These effects are likely to be most significant in species such as terrestrial orchids and lilies, in which all reproductive material may be consumed in a single visit, and those species whose reproductive effort is largely limited to the post-fire period (Keith 1996). While the magnitude of reductions in fecundity remain to be quantified under varying levels of browsing, our qualitative observations during reconnaissance suggest that the current densities of deer populations in the Jibbon/Bundeena area could be causing substantial reductions in seed production in a wide range of plant species.

A third life-cycle process susceptible to interruption by deer herbivory is the survival and growth of established plants. These effects are likely to be less significant in plant species that are capable of growth above the vertical reach of deer (c. 1.5-2.0 m). However, sustained herbivory could slow or block the transition from juvenile to mature growth forms and could also reduce survival in mature individuals if bark stripping occurs at levels observed in the enclosure experiment. These effects have resulted in failure of revegetation projects elsewhere in Royal National Park (e.g. Hacking River Valley) and in other parts of the world (Augustine

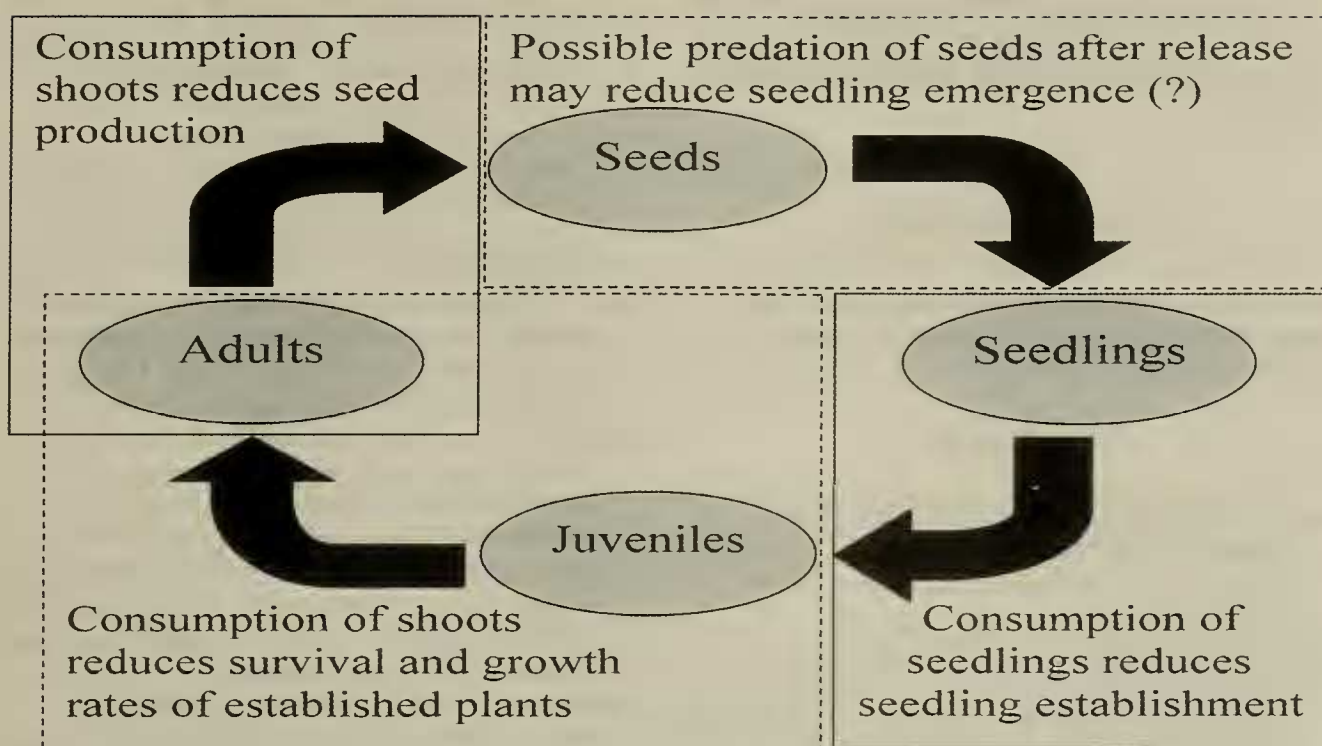


Figure 4. Simplified plant life cycle showing life history processes influenced by deer herbivory. Processes marked by unbroken lines are predicted to exert a greater influence on population viability than those marked by broken lines.

and Frelich 1998, Opperman and Merenlender 2000, Coomes et al. 2003), imposing substantial additional costs on the rehabilitation of degraded areas. Deer are also implicated in the predation of seeds after their release from plants. For example, the removal of *Telopea speciosissima* seeds from experimental caches coincided with deposition of deer faeces at the site (T. D. Auld and A. Denham, unpublished data). However, the magnitude of seed losses is unknown.

In wild populations, the impacts on survival and growth of established plants are likely to be less significant than effects on seedling recruitment and fruit production, but all three processes will have cumulative impacts on the population viability of many plant species. The magnitude of impacts for any given plant species will depend upon its palatability relative to other available forage, density of the deer population, the accessibility of edible plant tissues and the propensity to replace leaf tissue. The model (Fig. 4) nevertheless predicts the decline of many woody plant species and some herbaceous species because the recruitment of new seedlings fails to compensate for the attrition of established plants. This is supported by Moriarty's (2004b) observation that 30-70% fewer plant species occurred in understorey vegetation exposed to high deer densities compared with that

exposed to low deer densities. On the other hand, deer herbivory could favour the relatively few unpalatable plant species, particularly those ferns and sedges that may spread vegetatively to occupy space vacated by declines in densities of palatable shrubs and herbs. The abundance of *Pteridium esculentum* and relative scarcity of shrubs in forest understoreys adjacent to cleared grassy areas would seem consistent with this prediction. The predicted transformation of forest understoreys from structurally complex, floristically diverse assemblages to simple assemblages dominated by ferns and sedges is likely to reduce the suitability of habitats for a range of vertebrate and invertebrate fauna (Catling 1991, York 1999).

Reducing the density of deer populations may slow or reverse some effects of deer herbivory, as suggested by the observed recovery of surviving individuals of *Syzygium paniculatum* when deer were excluded from the treatment yard. Such effects have also been observed elsewhere (Anderson and Katz 1993, McShea and Rappole 2000). However, it is not known what level of deer control in the wild would produce such a response. Furthermore, the recovery of native vegetation would be impeded by deer-related soil erosion and compaction, or if densities of shrubs or their seed banks had already declined to very low

levels. Our model suggests that fire management and the control of deer after fire are likely to be crucial in managing impacts of deer herbivory on native vegetation.

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